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# BREEDING SWEET CORN RESISTANT TO THE CORN EARWORM

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## INTRODUCTION

The production of sweet corn (*Zea mays*) in the southern part of the United States and throughout the American Tropics is seriously interfered with by the ravages of the corn earworm (*Chloridea obsoleta* Fab.).

The geographic range of this insect is practically coextensive with maize culture, extending to the northern boundaries of the United States. But Quaintance and Brues[1] state that nowhere in the transition zone, comprising in the main the New England States, New York, Pennsylvania, Michigan, Wisconsin, and Minnesota, is the pest of regular occurrence or a cause of any considerable damage. For some distance south of this region the injury is also comparatively slight, but in many sections near the southern border of the country sweet corn is not grown at all, its place on the table being taken by field varieties.

The exclusion of sweet varieties from these regions may not be entirely due to the corn earworm, but it is probably safe to consider this insect the major factor.

The corn earworm does not confine its depredations to sweet corn, but also attacks field varieties. From the fact that northern varieties of field corn, when grown in the South suffer much more than do the local sorts, it would appear that the especial susceptibility of sweet varieties is not due to the character of the seeds alone, and that the southern varieties of field corn must possess some additional peculiarity that renders them at least partially immune.

A comparison of the general characteristics of northern and southern varieties at once suggests that the greater immunity of southern varieties may be due to the greater development of husks in the southern varieties. Attention was early called to this possibility by Mr. O. F. Cook,[2] from observations made on a variety of corn growing near Brownsville, Tex. This variety produces small ears inclosed in very long husks. Mr. Cook noticed that, while many larvæ were found inside of the projecting husks, few had reached the ears.

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[1] Quaintance, A. L., and Brues, C. T. the cotton bollworm. U. S. Dept. Agr. Bur. Ent. Bul. 50, 155 p., 27 fig., 25 pl., 1905.

[2] Bionomist in Charge, Office of Acclimatization and Adaptation of Crop Plants and Cotton Breeding, Bureau of Plant Industry.

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With the idea that southern field varieties owe their relative immunity to the thick covering of long husks which protect their ears, it seemed worth while to endeavor to breed varieties of sweet corn possessing numerous long husks. Since the distinctive character of the seeds of sweet varieties behaves in hybrids as a Mendelian unit, strains that would breed true to the sweet character might be expected in the second generation of a cross between field and sweet varieties. It was hoped that from the plants producing sweet seeds, strains possessing the desired husk characters could be isolated.

The present paper is an account of an attempt to secure this result, with a discussion of some of the factors of worm resistance on which light has been thrown in the course of the experiment.

Even in the worst worm-infested regions it is largely a matter of chance whether any particular ear is injured or escapes. To select intelligently, it is therefore highly important to know something of the plant characters that minimize injury and to use these characters as a basis for selection. The study of the characters associated with worm resistance was carried on simultaneously with the breeding work, and the value of the results is believed to lie in the analysis of the characters and the method of breeding quite as much as in the material results. These material results comprise two strains of sweet corn possessing marked resistance to the corn earworm.

## PROTECTIVE CHARACTERS

Four protective characters were in mind at the beginning of the experiment: (1) The distance which the husks extend beyond the tip of the ear, with the idea that larvæ frequently gain access to the ear by entering at the tip of the shoot and eating their way down the silks. It would obviously be advantageous to increase the distance they must travel. (2) The thickness of the husks' covering. Many ears are found with perforations through the husks, and a thicker covering might be expected to hinder the invasion of the larvæ from this direction. (3) The texture of the husks. In most sweet varieties the husks are relatively soft and smooth, while in field varieties, especially those from the Tropics, the husks are firm and harsh. The outer husks of some varieties are covered with firm spicules, providing a surface almost as silicious as sandpaper. This character might be expected to deter the insects from eating their way to the ear through the husks. (4) Husk leaves. It was thought that ears without husk leaves might be less attractive to moths.

## PLAN OF EXPERIMENTS

The experiments were begun in 1912. Mr. John H. Kinsler, at Victoria, Tex., made various crosses between three commercial varieties of sweet corn, Stowell's Evergreen, Early Evergreen, and Early Cory, and two varieties of field corn, Brownsville and Marrainto. Brownsville is

a selected strain of the variety in which Mr. O. F. Cook had first observed the worm resistance; Marrainto is a variety from northern Mexico, with rather thicker and harsher husks than those of Brownsville. These also extend well beyond the ear.

Isolated plantings of the first generation of these crosses were made at Victoria in 1913. The four lines which have been continued are Ph75 Brownsville × Early Cory; Ph77 Early Evergreen × Brownsville; Ph79, Stowell × Brownsville; and Ph80, Marrainto × Evergreen. The ears from the first-generation hybrid plants contained a mixture of sweet and horny seeds. The sweet seeds from selected ears of each of the four hybrids were planted in separate rows at Lanham, Md., in 1914, one row from each ear.

The procedure in 1914 was to make pollinations between plants of a similar appearance, and usually within the same row. The distance the husks extended beyond the ear, the thickness and number of husks, and the extent to which husk leaves were developed were recorded for all plants used in making pollinations. An attempt was also made to grade the plant with respect to the texture of the husks.[1] In selecting plants for pollination preference was given to those with long husks and few husk leaves; but other types were also pollinated, including a few that were distinctly inferior with respect to the characters thought to denote worm resistance.

Fourteen ears were selected for ear-to-row tests in 1915. The designations of these ears with their ancestry are given in Table I.

TABLE I.—*History of the corn plantings made at Chula Vista, Cal., in 1915*

| 1912. Victoria, Tex. Original cross. | 1913. Victoria, Tex. Treatment. | 1914. Lanham, Md. (Sweet seeds planted.) Plant combinations. | 1915. Chula Vista, Cal. Planting designation. |
|---|---|---|---|
| Brownsville × Early Cory | Isolated block | 121×122 | Ph121 |
| Do | do | 124×122 | Ph123 |
| Do | do | 1×9 | Ph127 |
| Do | do | 8×111 | Ph128 |
| Evergreen × Brownsville | Hand-pollinated | 10×12 | Ph129 |
| Do | do | 12×10 | Ph130 |
| Do | do | 12×15 | Ph131 |
| Stowells × Brownsville | Isolated block | 159×158 | Ph120 |
| Do | do | 137×75 | Ph122 |
| Do | do | 140×138 | Ph124 |
| Do | do | 89×30 | Ph125 |
| Do | do | 162×160 | Ph126 |
| Marrainto × Evergreen | Hand-pollinated | 182×179 | Ph118 |
| Evergreen × Brownsville | do | 32<br>×<br>21 | |
| Stowells × Brownsville | Isolated block | | Ph119 |

[1] The surface of the husks in the hybrid progenies is distinctly harsher than in commercial varieties of sweet corn. It was not found possible, however, to distinguish the different progenies in this particular with serviceable accuracy and the notation of the character has been discontinued.

The 1915 planting was made at Chula Vista, near San Diego, Cal., on March 15. The corn earworm is a more serious pest in this region than at Lanham, Md., and a more uniform infestation resulted.

In comparison with other plantings of sweet varieties in the same neighborhood, there seemed little doubt that the field of hybrids as a whole was less injured than other varieties. An effort was made, however, to secure definite quantitative data on the effect of the selection, and to determine the characters most closely associated with immunity. The characters of the individual plants were recorded in a series of measurements described below:

(1) DAMAGE.—The portion of the ear rendered inedible was estimated on a scale of 10—that is, an ear in which the larvæ had eaten completely to the base, rendering it worthless, was classed as 10. The slightest damage was recorded as 1 and an ear one-half of which was destroyed as 5. With intermediate stages estimated on the same scale, the grading was all done by the junior author and experiments showed that the maximum uncertainty regarding the class to which any particular ear should be referred was not greater than one grade.

(2) NUMBER OF LARVÆ.—The number of larvæ found inside the husks at harvest, together with any which it could be seen had escaped. When the infestation is very severe, the fact that the larvæ are cannibalistic would doubtless cause the recorded number to be lower than the true number.

(3) DAMAGE PER LARVA.—The figure indicating the total damage of each progeny divided by the total number of larvæ in the same progeny.

(4) PROLONGATION.—The distance from the tip of the ear to the tip of the husks, recorded in centimeters.

(5) LENGTH OF HUSKS.—This measurement was obtained by adding the prolongation and length of ear.

(6) LENGTH OF EAR.—The length of the ear in centimeters, including any damaged portion.

(7) NUMBER OF HUSKS.—The total number of husks surrounding the ear.

(8) NUMBER OF LAYERS.—A small hole was cut through the husks at the side of the ear at a point about midway between the tip and the base, and the number of layers of husks at this point were recorded.

(9) DAYS TO SILKING.—The number of days that elapsed from planting to the first appearance of silk.

(10) MATURITY.[1]—The degree of maturity was judged by slicing off the tops of the grains, and estimating the proportion of opaque to transparent endosperm. Prime eating condition was designated "grade 10." The lowest grade that would be marketable on our scale would be about 6 and the highest about 15.

(11) SILKING TO HARVEST.[1]—The number of days that elapsed between silking and harvesting of the ear.

(12) HUSK LEAVES.—The extent to which husk leaves were developed was graded in accordance with an arbitrary scale ranging from 0 to 10. The same system of grading husk leaves has been used for a number of years in recording the behavior of all varieties grown and has proved to be a reliable measurement.

(13) NUMBER OF ROWS.—The number of rows of grains on the ear was included in the notes largely as an indication of the circumference of the ear.

Table II gives the mean value of each of the characters for each of the progenies grown in 1915.

[1] Not taken in 1915.

TABLE II.—*Measurement of plant characters at Chula Vista, Cal., in 1915*

| Progeny. | Damage. | | Number of larvæ. | | Damage per larva. | | Prolongation. | |
|---|---|---|---|---|---|---|---|---|
| | First ears. | Second ears. | First ears. | Second ears. | First ears. | Second ears. | First ears. | Second ears. |
| Ph118 | 2.1±0.3 | 3.1±0.3 | 1.3±0.1 | 1.4±0.1 | 1.7±0.3 | 2.1±0.2 | 9.8±0.6 | 9.9±0.4 |
| Ph119 | 2.7± .3 | 1.6± .2 | 1.6± .2 | 1.2± .1 | 1.7± .3 | 1.3± .2 | 9.7± .5 | 10.9± .5 |
| Ph120 | 3.3± .6 | 1.9± .4 | 1.7± .2 | 1.2± .1 | 2.0± .5 | 1.5± .3 | 9.8± .6 | 9.8± .8 |
| Ph121 | 2.5± .3 | 1.6± .2 | 1.8± .2 | 1.5± .1 | 1.4± .2 | 1.1± .2 | 9.7± .2 | 9.8± .5 |
| Ph122 | 2.2± .2 | 1.4± .3 | 1.4± .1 | 1.3± .1 | 1.5± .2 | 1.1± .2 | 11.2± .3 | 11.6± .8 |
| Ph123 | 1.8± .3 | 1.5± .3 | 1.3± .1 | 1.3± .1 | 1.4± .9 | 1.2± .2 | 8.3± .4 | 8.7± .5 |
| Ph124 | .8± .2 | 1.9± .5 | 1.1± .1 | .8± .1 | .7± .2 | 2.3± .8 | 13.1± .6 | 11.9± .8 |
| Ph125 | 5.9± .8 | 4.6± .8 | 2.2± .1 | 2.0± .2 | 2.8± .4 | 2.3± .4 | 9.7± .5 | 8.1± .8 |
| Ph126 | 3.1± .3 | 4.4± .7 | 2.1± .1 | 1.8± .3 | 1.5± .2 | 2.4± .5 | 6.5± .4 | 7.8± .9 |
| Ph127 | 3.3± .5 | 4.3± .4 | 1.9± .2 | 2.1± .1 | 1.8± .3 | 2.1± .2 | 6.0± .7 | 5.2± .4 |
| Ph128 | 5.0± .8 | 3.1± .3 | 2.1± .1 | 1.8± .2 | 2.4± .4 | 1.7± .3 | 12.5± .6 | 11.9± .7 |
| Ph129 | 5.3±1.1 | 4.4± .8 | 2.3± .2 | 1.7± .2 | 2.3± .5 | 2.6± .5 | 7.7± .1 | 10.3± .7 |
| Ph130 | 3.1± .4 | 2.7± .3 | 1.7± .2 | 1.9± .2 | 1.9± .4 | 1.4± .2 | 8.9± .5 | 8.4± .4 |
| Ph131 | 3.8± .4 | 2.4± .3 | 1.9± .1 | 1.5± .1 | 2.0± .2 | 1.6± .2 | 7.3± .5 | 10.1± .6 |

| Progeny. | Length of ear, first ears. | Number of husks, first ears. | Number of layers. | | Days to silking, first ears. | Husk leaves. | | Number of rows, first ears. |
|---|---|---|---|---|---|---|---|---|
| | | | First ears. | Second ears. | | First ears. | Second ears. | |
| Ph118 | 13.1±0.3 | 12.7±0.3 | 10.7±0.3 | 10.0±0.2 | 98±1 | 2.8±0.3 | 3.3±0.2 | 14.0±0.2 |
| Ph119 | 14.7± .3 | 13.3± .4 | 10.0± .3 | 10.4± .3 | 108±1 | .6± .1 | 1.5± .2 | 15.0± .3 |
| Ph120 | 14.3± .5 | 16.4± .7 | 11.6± .4 | 12.2± .4 | 113±2 | 2.2± .4 | 2.7± .3 | 16.7± .4 |
| Ph121 | 14.3± .3 | 12.3± .4 | 8.8± .4 | 7.9± .3 | 107±1 | 4.3± .3 | 4.8± .4 | 12.4± .2 |
| Ph122 | 15.8± .3 | 14.1± .3 | 10.9± .2 | 12.2± .3 | 107±1 | .4± .1 | .9± .2 | 13.0± .2 |
| Ph123 | 15.4± .3 | 12.4± .3 | 10.6± .4 | 10.3± .2 | 105±1 | 1.8± .3 | 2.3± .2 | 13.2± .3 |
| Ph124 | 15.3± .4 | 13.7± .4 | 11.6± .5 | 10.9± .3 | 111±2 | .3± .2 | 1.2± .2 | 17.1± .4 |
| Ph125 | 15.6± .6 | 10.1± .4 | 8.7± .3 | 9.2± .9 | 96±2 | 1.1± .3 | 1.0± .3 | 14.8± .3 |
| Ph126 | 15.1± .5 | 12.8± .4 | 10.2± .4 | 12.1± .7 | 115±1 | 1.8± .3 | 1.6± .4 | 17.5± .5 |
| Ph127 | 11.9± .6 | 10.8± .6 | 7.3± .2 | 7.1± .5 | 104±3 | 1.4± .4 | 3.7± .5 | 13.6± .4 |
| Ph128 | 12.3± .4 | 11.7± .6 | 7.8± .5 | 8.4± .3 | 107±2 | 1.4± .4 | 2.8± .4 | 14.5± .2 |
| Ph129 | 14.7± .8 | 15.0± .4 | 10.0± .4 | 9.3± .5 | 92±4 | .7± .4 | 1.6± .2 | 15.3± .5 |
| Ph130 | 14.3± .3 | 14.7± .6 | 10.0± .2 | 9.4± .2 | 90±1 | 1.2± .2 | 3.9± .3 | 14.7± .3 |
| Ph131 | 14.0± .5 | 12.8± .6 | 9.1± .3 | 9.4± .3 | 103±2 | 1.2± .1 | 3.0± .3 | 13.1± .2 |

## ANALYSIS OF RESULTS IN 1915

The first step in analyzing the results was to determine whether the several rows showed real differences in the amount of damage inflicted by the corn earworm. If significant differences were not developed, it would hardly be worth while to proceed with selection.

The average damage for the different rows is shown in columns 2 and 3, Table II, together with the probable errors. It will be seen that some rows are damaged much more than others, and a consideration of the probable error shows that many of these differences may not be ascribed to chance. An analysis of the first, or upper ears, for which the data are more complete, shows that the row with the greatest amount of damage, Ph125, was damaged seven and one-half times as much as Ph124, which was the least affected.

It was thought possible that the degree of damage of the different rows might be influenced by their position in the field. The infestation might come from one side of the field and the rows nearest its source thus be more severely damaged. The arrangement of the progenies in the table corresponds with that in the field, and no general trend is apparent. It hap-

pens that the least and most damaged rows stood side by side near the middle of the field. If location was a factor, adjacent rows should, on the average, show a closer agreement in the extent of damage than pairs taken at random. On eliminating Ph129, which is the reciprocal of Ph130, the correlation between adjacent rows for the upper ears alone is $0.161 \pm 0.189$ and for upper and second ears combined $0.173 \pm 0.189$. There is, thus, little or no tendency for adjacent rows to be damaged to a similar extent, and position in the field seems not to be an important factor in causing the observed differences.

On the other hand, if the immunity which some of the rows enjoyed is due to plant characteristics, there should be some agreement between the degree of immunity of upper and second ears of the same row. A comparison of the value in columns 2 and 3, Table II, shows such an agreement. The row in which the upper ears were most damaged is also the row in which the second ears were most damaged. It can also be seen that the row with the least damage to the first ears has a very low damage in the second ears. Beyond these rather outstanding cases, the agreement or lack of agreement is not obvious from inspection. The correlation of damage between upper and second ears is believed to be a fair measure of this agreement; it was found to be $0.718 \pm 0.087$. This correlation alone would seem to establish the fact that the individuality of progenies is an important factor in determining the extent of damage. From the 1915 results we may safely conclude that there is something about the plants descended from certain ears which affords them an appreciable measure of protection. The next step was to determine, if possible, whether this protection could be referred to any of the recorded plant characters.

As soon as a detailed analysis of the 1915 data was attempted it became evident that there were sources of error that had not been adequately guarded against. The ears were not harvested at a uniform stage of development, and those left longer were more severely damaged. There were also many ears bagged to secure pure seed, and since the bagging was in a measure selective, it introduced another source of possible error. These disturbing factors made it appear unwise to place confidence in any detailed analysis of the 1915 data. These results will therefore be considered only in connection with the results of the following season.

## EXPERIMENTS IN 1916

The 1916 plantings were made at Lanham, Md., on May 14 and consisted of 35 rows, as follows: A repetition of the 14 progenies grown in 1915 (ancestry described on p. 551), 9 progenies from ears secured by hand pollinations within the rows of the progenies grown in 1915, 8 progenies from ears obtained by crosses between the rows in 1915, and 2 first-generation crosses between 1915 progenies and Hopi maize. There were

also included one row of Oregon Evergreen (P129), a commercial variety of sweet corn, and a row of New Century Wonder (P125), a commercial soft variety on the market as a table corn. The pedigrees of the progenies added to the 14 progenies that were repeated from 1915 are given in Table III.

TABLE III.—*Ancestry of progenies added to the experiment in 1916*

| 1916 designation of progeny. | Nature of pollination in 1915. | | | |
|---|---|---|---|---|
| | Pistillate parent. | | Staminate parent. | |
| | Plant No. | Progeny. | Plant No. | Progeny. |
| Ph119C1 | 3308 | Ph119 | Self. | .......... |
| Ph123C1 | 3529 | Ph123 | 3523 | Ph123 |
| Ph125C1 | 3609 | Ph125 | 3603 | Ph125 |
| Ph125C2 | 3625 | Ph125 | 3617 | Ph125 |
| Ph127C1 | 3718 | Ph127 | 3706 | Ph127 |
| Ph128C1 | 3776 | Ph128 | 3773 | Ph128 |
| Ph128C2 | 3773 | Ph128 | 3754 | Ph128 |
| Ph130C1 | 3865 | Ph130 | Self. | .......... |
| Ph132 | 3270 | Ph118 | 3323 | Ph119 |
| Ph133 | 3330 | Ph119 | 3601 | Ph125 |
| Ph134 | 3334 | Ph119 | 3286 | Ph118 |
| Ph135 | 3368 | Ph120 | 3328 | Ph119 |
| Ph136 | 3369 | Ph120 | 3328 | Ph119 |
| Ph137 | 3373 | Ph120 | 21 | Hopi. |
| Ph138 | 3403 | Ph121 | 3328 | Ph119 |
| Ph139 | 3489 | Ph122 | 3320 | Ph119 |
| Ph140 | 3557 | Ph124 | 3523 | Ph123 |
| Ph141 | 3602 | Ph125 | 21 | Hopi. |

The method of taking notes has already been described (p. 552). The same procedure was followed as in 1915, except that the number of days from silking to harvest and the degree of maturity were added.

To make it possible to secure ears at approximately the same degree of maturity, the exact dates of the first pollen and the first appearance of silks were recorded on a tag attached to each plant. After a few preliminary experiments it was found that from 16 to 18 days after silking the ears were in prime eating condition. The attempt was made, therefore, to harvest all ears within these dates. There was some deviation from this rule, but the results showed that these departures did not materially affect the damage.

Table IV gives the mean values of the characters (first and second ears combined) for each of the progenies, with the probable errors of the determinations. As in 1915, the order of the progenies in the table is the same as that in which they were planted.

The 14 original progenies, which are repetitions of the 1915 series, are marked with an asterisk. The 1915 ancestry of the new progenies is given in Table III, but to trace the ancestry back of 1915 reference may be made to Table I.

TABLE IV.—*Mean of different characters of corn, first and second years combined, in 1916*

| Progeny. | Number of plants. | Damage. | Number of larvæ. | Damage per larva. | Prolongation. | Length of husks. | Length of ear. | Number of husks. | Number of layers. | Days to silking. | Maturity. | Days silking to harvest. | Husk leaves. | Number of rows. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *Grades.* | | *Grades.* | *Cm.* | *Cm.* | *Cm.* | | | | *Grades.* | | *Grades.* | |
| P125 | 79 | 0.63±0.07 | 0.72±0.04 | 1.14±0.15 | 3.75±0.27 | 28.9±0.24 | 25.0±0.21 | 11.4±0.19 | 9.31±0.14 | 89.0±0.35 | 12.0±0.17 | 18.9±0.23 | 2.29±0.12 | 12.3±0.11 |
| P129 | 47 | 1.11± .10 | .89± .06 | 1.24± .14 | 5.61± .48 | 26.1± .46 | 26.2± .39 | 13.8± .30 | 7.68± .13 | 80.9± .36 | 9.7± .18 | 16.4± .08 | 5.42± .20 | 13.8± .15 |
| *Ph118 | 64 | .50± .08 | .72± .04 | .70± .12 | 7.14± .19 | 25.2± .24 | 18.2± .24 | 13.0± .16 | 9.67± .21 | 85.0± .34 | 11.5± .13 | 17.7± .11 | 4.53± .18 | 13.6± .13 |
| *Ph119 | 68 | .28± .05 | .60± .04 | .46± .14 | 8.75± .36 | 27.4± .32 | 18.8± .19 | 13.9± .22 | 9.65± .17 | 82.2± .32 | 10.1± .14 | 17.2± .14 | 2.95± .14 | 15.3± .15 |
| Ph119C1 | 47 | .47± .09 | .62± .06 | .76± .20 | 10.20± .47 | 25.6± .25 | 15.2± .22 | 11.0± .20 | 8.20± .16 | 80.7± .18 | 9.4± .22 | 16.4± .57 | 1.68± .18 | 12.4± .14 |
| *Ph120 | 51 | .39± .09 | .76± .04 | .51± .12 | 7.57± .33 | 27.6± .33 | 20.1± .25 | 15.5± .32 | 11.20± .15 | 87.0± .42 | 11.1± .14 | 17.2± .14 | 2.10± .13 | 17.6± .22 |
| *Ph121 | 65 | .97± .06 | .86± .03 | 1.12± .08 | 4.06± .28 | 24.8± .24 | 21.0± .17 | 15.5± .21 | 10.60± .16 | 84.3± .34 | 10.9± .12 | 17.1± .16 | 4.10± .14 | 13.5± .19 |
| *Ph122 | 71 | .51± .07 | .76± .03 | .67± .09 | 5.50± .30 | 26.8± .27 | 21.5± .20 | 15.2± .20 | 10.60± .14 | 84.4± .28 | 10.6± .11 | 17.2± .06 | 2.53± .14 | 14.2± .12 |
| *Ph123 | 66 | .58± .07 | .68± .05 | .85± .13 | 5.06± .30 | 25.5± .21 | 20.3± .19 | 11.9± .16 | 9.57± .15 | 83.6± .38 | 10.7± .09 | 16.8± .08 | 2.40± .10 | 13.1± .13 |
| Ph123C1 | 55 | .76± .06 | .87± .04 | .88± .08 | 2.38± .25 | 22.9± .22 | 20.2± .20 | 11.1± .18 | 8.30± .15 | 84.0± .33 | 11.0± .11 | 16.8± .10 | 2.96± .12 | 12.1± .09 |
| *Ph124 | 27 | .04± .01 | .37± .10 | .10± .03 | 10.80± .43 | 30.4± .43 | 19.0± .30 | 14.7± .32 | 1.12± .24 | 85.3± .48 | 10.5± .15 | 17.2± .09 | 1.37± .10 | 18.3± .32 |
| *Ph125 | 44 | .45± .08 | 1.02± .06 | .45± .09 | 8.04± .58 | 29.0± .34 | 21.3± .50 | 11.9± .27 | 9.10± .19 | 79.0± .44 | 10.6± .27 | 16.3± .06 | 5.73± .23 | 15.3± .23 |
| Ph125C1 | 63 | .71± .08 | .84± .05 | .85± .11 | 6.76± .25 | 26.8± .25 | 20.0± .26 | 12.6± .20 | 8.90± .16 | 78.0± .38 | 9.8± .13 | 16.6± .08 | 4.85± .22 | 15.1± .24 |
| Ph125C2 | 22 | 1.00± .18 | .96± .08 | 1.05± .20 | 4.68± .50 | 26.9± .58 | 22.4± .34 | 12.1± .29 | 8.90± .31 | 83.0± .84 | 10.1± .34 | 17.1± .23 | 2.77± .30 | 15.4± .36 |
| *Ph126 | 55 | .91± .08 | .73± .05 | 1.25± .15 | 3.68± .27 | 24.3± .24 | 20.2± .35 | 11.9± .21 | 8.84± .18 | 90.1± .53 | 12.4± .29 | 19.3± .34 | 3.12± .13 | 17.3± .10 |
| *Ph127 | 67 | 1.19± .09 | 1.13± .07 | 1.04± .10 | 2.94± .22 | 22.9± .25 | 19.6± .24 | 13.2± .19 | 8.20± .15 | 79.0± .38 | 9.5± .11 | 16.4± .06 | 5.30± .18 | 14.7± .17 |
| Ph127C1 | 45 | 1.93± .18 | 1.18± .08 | 1.64± .20 | 2.69± .32 | 21.9± .39 | 18.8± .23 | 13.1± .21 | 7.87± .17 | 78.4± .52 | 9.8± .16 | 16.5± .05 | 3.69± .13 | 14.9± .23 |
| *Ph128 | 86 | .45± .06 | .65± .04 | .70± .11 | 9.16± .31 | 30.4± .26 | 21.2± .21 | 13.3± .20 | 9.70± .14 | 81.0± .27 | 10.6± .12 | 17.2± .14 | 4.14± .15 | 16.3± .14 |
| Ph128C1 | 70 | .29± .09 | .52± .06 | .56± .19 | 12.00± .29 | 29.9± .33 | 18.1± .19 | 13.8± .23 | 9.09± .15 | 83.0± .43 | 10.9± .12 | 17.4± .10 | 3.50± .18 | 15.7± .17 |
| Ph128C2 | 18 | 1.39± .31 | .95± .11 | 1.47± .37 | 11.60± .76 | 31.6± .57 | 19.8± .32 | 13.4± .28 | 10.20± .28 | 80.9± .82 | 10.4± .19 | 16.5± .11 | 3.56± .20 | 15.5± .43 |
| *Ph129 | 54 | 1.13± .10 | 1.11± .07 | 1.01± .11 | 5.05± .22 | 24.0± .26 | 19.0± .22 | 13.3± .21 | 8.76± .18 | 75.1± .30 | 9.4± .14 | 16.1± .02 | 4.93± .26 | 15.6± .22 |
| *Ph130 | 85 | 1.10± .07 | 1.14± .04 | .97± .07 | 5.40± .20 | 24.4± .24 | 19.0± .20 | 14.6± .18 | 9.15± .15 | 74.5± .27 | 8.8± .16 | 15.9± .08 | 5.71± .20 | 15.6± .14 |
| Ph130C1 | 70 | .95± .08 | 1.03± .04 | .92± .09 | 6.70± .27 | 22.7± .25 | 15.8± .24 | 13.1± .16 | 8.95± .14 | 75.7± .37 | 9.2± .14 | 16.1± .04 | 4.27± .22 | 16.3± .10 |
| Ph130C2 | 78 | .87± .05 | .99± .03 | .88± .06 | 5.97± .26 | 25.1± .19 | 19.0± .21 | 12.6± .16 | 8.80± .14 | 76.7± .26 | 9.8± .03 | 16.6± .09 | 3.90± .19 | 16.6± .14 |
| *Ph131 | 68 | .96± .08 | 1.15± .03 | .83± .07 | 5.95± .25 | 24.3± .19 | 18.3± .21 | 15.1± .22 | 9.50± .16 | 74.2± .25 | 8.6± .16 | 15.9± .09 | 4.22± .20 | 14.9± .15 |
| Ph132 | 99 | .33± .03 | .50± .05 | .67± .14 | 7.65± .22 | 25.8± .27 | 18.2± .14 | 12.1± .14 | 8.64± .12 | 79.1± .26 | 10.4± .06 | 16.6± .06 | 4.10± .14 | 13.9± .11 |
| Ph133 | 35 | .34± .05 | .71± .07 | .50± .19 | 6.80± .38 | 28.9± .42 | 22.1± .32 | 13.3± .34 | 9.82± .24 | 81.0± .64 | 9.3± .27 | 16.7± .14 | 4.34± .30 | 15.8± .20 |
| Ph134 | 67 | .36± .03 | .52± .06 | .69± .20 | 10.30± .30 | 27.9± .30 | 17.6± .22 | 13.9± .20 | 10.40± .16 | 79.8± .34 | 10.3± .07 | 16.4± .04 | 3.58± .21 | 14.0± .15 |
| Ph135 | 62 | .65± .08 | .65± .04 | 1.00± .14 | 4.10± .24 | 24.5± .22 | 20.4± .18 | 17.7± .35 | 12.10± .19 | 83.8± .32 | 10.9± .14 | 17.3± .15 | 2.59± .13 | 16.4± .19 |
| Ph136 | 30 | .57± .11 | .67± .06 | .85± .18 | 5.16± .47 | 24.0± .37 | 18.5± .23 | 17.2± .45 | 10.70± .36 | 84.2± .45 | 11.1± .11 | 17.2± .13 | 2.80± .22 | 15.7± .32 |
| Ph137 | 60 | 1.37± .10 | 1.11± .05 | 1.22± .11 | 5.06± .33 | 27.4± .27 | 22.6± .36 | 15.6± .28 | 9.70± .18 | 78.1± .37 | 10.6± .15 | 17.4± .18 | 4.20± .17 | 18.3± .17 |
| Ph138 | 91 | .74± .06 | .66± .04 | 1.11± .11 | 3.04± .22 | 26.1± .21 | 23.1± .17 | 16.3± .20 | 10.80± .14 | 83.8± .27 | 11.2± .07 | 16.9± .08 | 2.90± .09 | 15.4± .13 |
| Ph139 | 63 | .48± .05 | .76± .05 | .63± .11 | 7.98± .28 | 26.1± .22 | 18.2± .20 | 16.0± .22 | 10.50± .15 | 78.3± .27 | 9.8± .12 | 16.1± .02 | 3.80± .20 | 15.1± .15 |
| Ph140 | 28 | .07± .01 | .50± .10 | .14± .30 | 9.25± .46 | 29.4± .52 | 20.2± .30 | 14.4± .40 | 10.00± .25 | 80.6± .36 | 10.0± .12 | 16.2± .04 | 3.32± .19 | 15.7± .16 |
| Ph141 | 54 | 1.28± .09 | 1.37± .06 | .93± .08 | 3.67± .37 | 30.2± .26 | 26.7± .40 | 12.9± .23 | 9.10± .18 | 78.0± .39 | 9.8± .14 | 16.3± .04 | 3.80± .18 | 16.0± .21 |

* 1915 progeny.

## DISCUSSION OF RESULTS

The results of the 1916 experiments will first be examined to determine whether they corroborate the 1915 data in showing that there are significant differences among the progenies in the extent of damage.

An examination of the average damage of the different progenies (Table IV, column 2) shows the results to be in fair accord with those of the previous year and shows even more clearly that the differences in the extent of damage are not the result of accident.

Ph124, again the least damaged of all the progenies, is with one exception separated from all other progenies by significant differences. The exception, Ph140, is a descendant of Ph124, produced in 1915, the male parent being a plant of Ph123. From the remaining progenies Ph124 is separated by differences that range from 2.4 to 16.5 times the probable error.

It may be seen also that Oregon Evergreen, P129, one of the commercial varieties included in the experiment, was damaged more than any of the hybrid progenies except Ph127, Ph127C1, and Ph128C2. One of these, Ph127C1, is the only progeny in which the difference is significant. Oregon Evergreen was chosen for comparison as one of the most worm-resistant of the commercial varieties of sweet corn. It is also the variety most generally grown in the worm-infested regions of the Southwest. The relatively high damage in the two Hopi hybrids Ph137 and Ph141 should also be noted. The following notes were taken on an Eastern variety of sweet corn grown by the side of the wormproof corn experiment and maturing at the same time.

| | |
|---|---|
| Prolongation | $2.0 \pm 0.2$ |
| Number of larvæ | $2.4 \pm .1$ |
| Damage | $3.8 \pm .4$ |
| Degree of maturity | $8.9 \pm .4$ |

Since the days from silking to harvest were not recorded for the variety, it is not included in Table IV. The degree of maturity was lower than in any of the wormproof progenies, and, since damage is negatively correlated with maturity, the comparison is believed to be in no way unfair. The damage to this variety was nearly 3 times that of the wormproof progeny with the greatest damage, and 29 times that of the progeny least damaged. As a further comparison the average damage to Golden Bantam sweet corn growing in a garden about ¼ mile from the experiment was found to be $2.6 \pm 0.5$.

Considering only the 14 rows planted from the same lots of seed as the 1915 experiment (marked with an asterisk in Table IV), it will be seen that the row least damaged in 1915 was also the least damaged in 1916. Beyond this, while it can be seen that there is a general agreement, there are many changes in the standing of the progenies. Most of these differences are doubtless to be ascribed to chance variations, for the determinations are by their nature subject to wide fluctuations. It should be kept in mind, however, that the two experiments were tried

in opposite parts of the continent and under widely different environmental conditions. It may well be that the dry, cool climate of the coast of California, where corn is grown under irrigation, would bring into prominence a somewhat different complex of protective factors than the relatively hot, moist climate of Maryland.

Table V gives the general average of the 14 progenies that were planted both seasons with respect to the different characters based on the upper ears and the interannual correlations for the different characters. It will be seen that the infestation was much more severe at Chula Vista, Cal., than at Lanham, Md. This is best indicated by the average number of larvæ. The damage per larva and the total damage were both increased at Chula Vista by the fact that in 1915 many of the ears were allowed to mature before the notes were taken. The pronounced environmental differences between the two localities is indicated by the fact that the time from planting to silking was, on the average, 23 days longer at Chula Vista than at Lanham the following year. In view of the much slower growth of the plants at Chula Vista, it is reasonable to assume that the grains were also slower in maturing. This would expose the ears to the attacks of the larvæ for a longer time and would tend to increase the damage per larva and total damage.

TABLE V.—*General mean of the different characters of 14 progenies in 1915 and 1916 and the interannual correlation*

| Factor. | Damage. | Number of larvæ. | Damage per larva. | Prolongation. | Length of husks. | Length of ear. |
|---|---|---|---|---|---|---|
| | | | *Grades.* | *Cm.* | *Cm.* | *Cm.* |
| General mean, 1915 | 3.22 | 1.75 | 1.76 | 9.32 | 23.6 | 14.3 |
| General mean, 1916 | .65 | .84 | .76 | 5.88 | 26.6 | 20.7 |
| Interannual correlation | .37±0.16 | .73±0.09 | .38±0.16 | .79±0.07 | .76±0.08 | .02±0.19 |

| Factor. | Number of husks. | Number of layers. | Days to silking. | Husk leaves. | Number of rows. |
|---|---|---|---|---|---|
| | | | | *Grades.* | |
| General mean, 1915 | 12.9 | 9.8 | 105.2 | 1.55 | 14.6 |
| General mean, 1916 | 12.7 | 9.9 | 82.0 | 3.24 | 15.3 |
| Interannual correlation | .53±0.13 | .62±0.11 | .51±0.13 | .39±0.16 | .72±0.09 |

Seventeen of the progenies grown in 1916 were descended from the fourteen progenies grown in 1915. The behavior of these progenies affords some evidence regarding the intensity of the inheritance of the measured characters. To reduce the agreement between parent and offspring to a quantitative basis, the mean values of the seventeen progenies and the mean values of their parent progenies, both grown in 1916, were correlated. Eight of the new progenies grown in 1916 were not descended from single 1915 progenies, but resulted from crosses between different 1915 progenies. In these cases a midparental value was taken by averaging the mean values of the two parents. The correlation coefficients are given in Table VI.

All of the correlations are positive and all are apparently significant. The average of the coefficients for the 11 measured characters was 0.60.

With such small numbers little confidence can be placed in differences in the correlations found for the different characters. It is interesting, however, that damage and number of larvæ have coefficients as large as those of morphological characters.

TABLE VI.—*Correlations between parents and offspring in corn experiments in 1916*

| Damage. | Number of larvæ. | Damage per larva. | Prolongation. | Length of husks. | Length of ear. |
|---|---|---|---|---|---|
| 0.66±0.09 | 0.72±0.09 | *Grades.* 0.40±0.14 | *Cm.* 0.68±0.09 | *Cm.* 0.72±0.09 | *Cm.* 0.56±0.11 |

| Number of husks. | Number of layers. | Days to silking. | Husk leaves. | Number of rows. | Average. |
|---|---|---|---|---|---|
| 0.46±0.13 | 0.43±0.13 | 0.61±0.10 | *Grades.* 0.53±0.12 | 0.77±0.12 | 0.60 |

## MEASURES OF INJURY

Of the characters recorded, three were measures of injury. These are given under the headings "Damage," "Damage per larva," and "Number of larvæ." As might be expected from the nature of the characters, the three measures of injury constitute a closely correlated group. The damage per larva was calculated by dividing the total amount of damage in each progeny by the total number of larvæ. The damage per larva is thus, of course, definitely associated with both damage and number of larvæ. There is, however, a factor in the degree of damage not covered by the two other characters—that is, the number of ears that escape without infestation. These uninfested ears reduce the average damage but do not affect the damage per larva.

Since to lessen the amount of damage is the practical object sought, primary consideration will be given to the relations existing between this character and possible protective characters. The correlations with number of larvæ and damage per larva will be considered only as they may help to elucidate the correlations with damage.

## CHARACTERS CORRELATED WITH INJURY

In Table VII are given the interprogeny correlations of the characters measured.

With 31 progenies little significance may be attached to any correlation that is less than 0.35, since to exceed 3 times the probable error the correlation must be at least 0.33. Of the plant characters measured, the following showed a correlation with damage of 0.35 or closer: prolongation, length of husks, number of layers, and days to silking. In addition to these, maturity and husk leaves are significantly correlated with number of larvæ. Among the plant characters the following significant correlations appear: Prolongation with length of husks; length of husks with length of ear; number of husks with number of layers; number of layers with days to silking; days to silking with maturity, days silking to harvest, and husk leaves; maturity with days to harvest and husk leaves.

TABLE VII—*Interprogeny correlations*

| Factor. | Damage. | Number of larvæ. | Damage per larva. | Prolongation. | Length of husks. | Length of ear. | Number of husks. | Number of layers. | Days to silking. | Maturity. | Days silking to harvest. | Husk leaves. | Number of rows. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | *Grades.* | *Cm.* | *Cm.* | *Cm.* | | | | *Grades.* | | *Grades.* | |
| Damage | .......... | 0.85±0.03 | 0.88±0.03 | −0.71±0.06 | −0.68±0.07 | 0.01±0.12 | −0.08±0.12 | −0.52±0.09 | −0.36±0.10 | −0.32±0.11 | −0.03±0.12 | 0.31±0.11 | 0.05±0.12 |
| Number of larvæ | 0.85±0.03 | .......... | .64± .07 | − .60± .08 | − .56± .08 | .03± .12 | − .15± .12 | − .51± .09 | − .56± .09 | − .49± .09 | − .25± .12 | .52± .09 | −.16± .12 |
| Damage per larva | .88± .03 | .64± .07 | .......... | − .75± .05 | − .78± .05 | .06± .12 | − .01± .12 | − .45± .10 | − .12± .12 | − .04± .12 | − .12± .12 | .12± .12 | −.16± .12 |
| Prolongation | −.71± .06 | −.60± .08 | −.75± .05 | .......... | .75± .06 | −.30± .11 | − .10± .12 | .25± .12 | − .02± .12 | − .07± .12 | − .04± .12 | −.13± .12 | .15± .12 |
| Length of husks | −.68± .07 | −.56± .08 | − 78± .05 | .75± .06 | .......... | .35± .11 | − .17± .12 | .27± .11 | .18± .12 | .06± .12 | .00± .12 | −.08± .12 | .15± .12 |
| Length of ear | .01± .12 | .03± .12 | .06± .12 | − .30± .11 | .35± .11 | .......... | .09± .12 | .11± .12 | .23± .12 | .27± .11 | .06± .12 | .08± .12 | .04± .12 |
| Number of husks | −.08± .12 | −.15± .12 | −.01± .12 | − .10± .12 | − .17± .12 | .09± .12 | .......... | .68± .07 | .05± .12 | .04± .12 | − .13± .12 | −.08± .12 | .28± .11 |
| Number of layers | −.52± .09 | −.51± .09 | −.45± .10 | .25± .12 | .27± .11 | .11± .12 | .68± .07 | .......... | .35± .11 | .33± .11 | .06± .12 | −.30± .11 | .33± .11 |
| Days to silking | −.36± .10 | −.56± .09 | −.12± .12 | − .02± .12 | .18± .12 | .23± .12 | .05± .12 | .35± .11 | .......... | .92± .02 | .66± .07 | −.56± .09 | .10± .12 |
| Maturity | −.32± .11 | −.49± .09 | −.04± .12 | − .07± .12 | .06± .12 | .27± .11 | .04± .12 | .33± .11 | .92± .02 | .......... | .60± .08 | −.35± .11 | .02± .12 |
| Days silking to harvest | −.03± .12 | −.25± .12 | −.12± .12 | − .04± .12 | .00± .12 | .06± .12 | − .13± .12 | .06± .12 | .66± .07 | .60± .08 | .......... | −.21± .12 | .22± .12 |
| Husk leaves | .31± .11 | .52± .09 | .12± .12 | − .13± .12 | − .08± .12 | .08± .12 | − .08± .12 | − .30± .11 | − .56± .09 | − .35± .11 | − .21± .12 | .......... | −.08± .12 |
| Number of rows | .05± .12 | −.16± .12 | −.16± .12 | .15± .12 | .15± .12 | .04± .12 | .28± .11 | .33± .11 | .10± .12 | .02± .12 | .22± .12 | −.08± .12 | .......... |

PROLONGATION OF HUSKS

The distance from the tip of the husks to the tip of the ear—in other words, the distance which the newly hatched larva, if it enters the tip of the husks, must travel before its depredations affect the ear—was first considered. This was the character thought to have been the chief cause of the immunity in the field varieties used as parents.

Of all the characters measured this proved to be the most closely correlated with damage and the number of larvæ, in both instances the correlation being negative. The interprogeny correlation between prolongation and damage was $-0.71 \pm 0.06$ and the regression of damage on prolongation was 1.02—that is, with an average increase of 1 cm. in the prolongation an additional 1 per cent of the crop was saved. The meaning of this regression of 1.02 may be further examined by comparing the damage in the progenies with the greatest and least prolongation. There were 14 progenies whose mean prolongation was less than 5 cm., the average prolongation of this group being 2.9 cm. The average damage in this group of progenies was one grade, or 10 per cent of the total crop. The 12 progenies with the greatest average prolongation, all of which were 6 cm. or over, had an average prolongation of 7.7 cm. and a damage of 0.5 grades, or 5 per cent. Thus, an average increase of 4.8 cm. in prolongation was accompanied by an average reduction of 5 per cent in damage.

The correlation of 0.71 between prolongation and damage is sufficiently close to justify the hope that the method followed is satisfactory and that by increasing the prolongation through hybridization or selection substantial reductions in the damage can be secured. A closer study, however, indicates that the relatively close correlation between prolongation and damage is probably not to be completely explained on the basis of a simple physical protection. The chief reason for doubting the apparent direct relation between prolongation and damage is that prolongation appears to have nearly as much affect on the number of larvæ as on the amount of damage, the correlation being $-0.60 \pm 0.08$. Since all the larvæ found inside the husks were counted, whether they had gained access to the ear or not, prolongation can hardly be held to have reduced the number of larvæ in any such manner as it might be expected to reduce the damage.

If, to gain access to the ear, the larva must eat its way down the silks, prolongation would seem necessarily to be a very effective protection. If, on the other hand, larvæ may force their way between the silks and simply crawl to the ear, prolongation would be much less effective. A very large proportion of the eggs are laid on the silks soon after they appear. The eggs hatch in two or three days and the newly hatched larvæ are only about 1.5 mm. long.[1] From the fact that

[1] Quaintance A. L., and Brues, C. T. Op. cit.

small larvæ are frequently found among the silks inside the husks with no indication of having eaten their way there, it is inferred that these small worms can crawl down the silks to the tip of the ear. Larvæ hatched on other parts of the plant would on the average be larger when they reach the silks and must eat their way to the ear. Against these larger larvæ a greater prolongation should prove an adequate protection, but they are a comparatively small factor in the total damage, as their depredations are largely confined to the tip of the ear.

In both 1915 and 1916 an attempt was made to record for each ear whether the larvæ entered the ear by traveling down the silks or by eating through the husks. Of the 1,449 earworms found in the damaged ears 1,384 were recorded as having entered from the end and only 65, or 4.5 per cent, by penetrating the husks. The holes so frequently observed in the husks, the presence of which led to the belief that thick, harsh husks would afford protection, are explained as being made by the larvæ when emerging. The few larvæ which gain access to the ear by eating through the husks do not leave a continuous track, for the husks of a young ear are elongating at different rates and the continuity of the hole left by the larva is soon broken.

From the fact that in the compacted silks the larvæ would be close together and the débris left by one larva might conceal other small larvæ, it was thought that there would perhaps be a greater tendency to overlook larvæ in the ears with great prolongation with the result that the number of larvæ in such ears would be underestimated. If errors of this kind were of sufficient magnitude, they might account for the correlation between prolongation and number of larvæ.

As a check against errors in counting the number of larvæ, the percentage of ears that had no larvæ was correlated with prolongation. Whatever may be the difficulties in counting the larvæ, whether an ear contains larvæ or not is a fact easily observed, and in dividing the ears into those with and those without larvæ there would be no tendency to overlook the presence of larvæ in ears with the greater prolongation. The correlation between prolongation and the percentage of ears with larvæ was found to be $-0.59$, a very close agreement with the $-0.60$ correlation between number of larvæ and prolongation.

If the relation between prolongation and damage as measured by the interprogeny regression is one of cause and effect—that is, if each increase of a centimeter actually reduces the damage by 1 per cent, the same relation should hold among the individual plants of a progeny. In other words, the intraprogeny regression should be the same as the interprogeny regression. The average intraprogeny correlation of damage and prolongation, which seems the best expression we have for the relations

existing among individuals, is $-0.254 \pm 0.024$ and the intraprogeny regression of damage on prolongation is 0.72.[1]

The apparent effect of prolongation on damage within the progeny is thus found to be only about 70 per cent of the effect indicated by the interprogeny regression.

The closer relation found to exist among the means of the progenies might come about through the interprogeny correlation of prolongation with other protective factors. The general absence of genetic correlations in maize characters would render this explanation improbable, but any explanation of the relation of prolongation to damage should also apply to the relation between prolongation and number of larvæ. It is not clear how prolongation can directly affect the number of larvæ, and the coherence of prolongation with other protective characters is the only explanation that suggests itself. For example, the progenies with the greatest prolongation might be later in maturing. If this were the case and larvæ became less numerous as the season advanced, the closeness of the interprogeny correlation between prolongation and damage would appear to be greater than it really is. To approximate the true effect of prolongation on damage, an attempt must be made to eliminate, as far as possible, the effects of other correlated characters. To do this, resort may be had to "partial correlations."

In the present example the partial correlation between prolongation and damage with respect to days to silking will give, so far as the data permit, the degree of relationship between prolongation and damage

[1] There are many difficulties in the way of securing a satisfactory expression for the intraprogeny correlations of damage and prolongation.

To combine the crude determinations of all the individuals into a single population is to confuse the inter- and intra-progeny correlations. To avoid this it seems better to calculate the intraprogeny correlation for each of the progenies.

There is a further difficulty in the choice of method. The customary product moment method, which is perfectly applicable to the means of the progenies, can not properly be used with the individuals of a single progeny owing to the pronounced skewness of the distribution of damage. In a great many of the progenies approximately one-half of the individuals have zero damage. This division of the plants into two groups, those that were damaged and those that were not, would seem to indicate that the biserial correlation may properly be used.

Differences between the mean prolongation of first and second ears prevent the combining of first and second ears in a single correlation table, but the independent calculation of the coefficient for first and second ears in the separate progenies provides an added check on the reliability of the method.

The method followed has been to calculate the biserial correlation in each of the progenies for both first and second ears. In most of the progenies the division was made between zero damage and a damage of one or more. In a few progenies a more equal division was secured by making the division between palants with a damage of one or less and two or more. No correlation was calculated where the smallest class fell below 10 individuals.

A weighted average of all the coefficients is taken as the best single expression of the intraprogeny correlation.

The mean intraprogeny regression was calculated by the formula. Regression of damage on prolongation=

$$Rdp\frac{\sigma d}{\sigma p}$$

where $Rdp$=average intraprogeny biserial correlation and $\sigma d$ and $\sigma p$=the square root of the mean of the weighted squares of the standard deviations.

for constant days to silking—that is, with the differences due to season eliminated.[1]

Damage does become somewhat less as the season advances, $r = -0.36$, but there is also a very slight tendency for the progenies with the longer season to have shorter prolongation, $r = -0.02$. The partial correlation of prolongation and damage for constant days to silking is $-0.76$. Since the direct correlation is $-0.71$, the conclusion is that among progenies with the same days to silking the negative correlation between prolongation and damage is, if anything, higher than is indicated by the direct correlation.

The effect of days to silking on the correlations between prolongation and the other measurements of injury are all in the same direction—that is, any effect which days to silking may have had is to make the apparent relationship less close than the true one. The partial correlations for constant days to silking change the direct correlation between prolongation and number of larvæ from $-0.60$ to $-0.73$, that between prolongation and damage per larva from $-0.75$ to $-0.76$.

In like manner the elimination of difference in "maturity" and "silking to harvest" fails to reduce the correlation between prolongation and the measures of injury. The partial correlation of prolongation and damage for constant maturity raises the direct correlation from $-0.71$ to $-0.79$; when constant for "silking to harvest," the direct correlation is unchanged.

Another character that might be suspected of affecting the relation between prolongation and damage is husk leaves. The presence of husk leaves may make the ears either more or less attractive to moths when they are depositing their eggs and thus change the number of larvæ gaining access to the ear.

The partial correlation between prolongation and damage for constant husk leaves indicates that the net result is negligible, since it reduces the direct correlation of $-0.71$ to only $-0.70$.

By applying the formula for partial correlations a second, third, and fourth time an expression may be obtained for the correlation between prolongation and damage with season, maturity, "silking to harvest," and husk leaves all constant. This was found to be $-0.83$. The writers therefore conclude that if the relatively close interprogeny correlation between prolongation and damage is due to the association of prolongation with other protective characters, these characters were not included in the notes.

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[1] The formula for partial correlations is $r_{12.3} = \frac{r_{12} - (r_{13} x r_{23})}{\sqrt{1 - r_{13}^2 x\ 1 - r_{23}^2}}$

where $r_{12}$ = correlation between variables 1 and 2,
$r_{13}$ = correlation between variables 1 and 3,
$r_{23}$ = correlation between variables 2 and 3,
and $r_{12.3} = r_{12}$ for constant 3.

The difference between the intra- and inter-progeny regression remains unexplained, and in the light of this disparity it should be kept in mind, no asurance can be given that an increase in the prolongation in other stocks will be followed by the same rapid increase in immunity found in the course of these experiments.

### LENGTH OF HUSKS

Length of husks and prolongation are measurements of nearly the same thing. Prolongation, however, may increase in either of two ways. The husks may be longer or the ear may be shorter. The first selections were made for prolongation without special regard to the length of the ear, and it was feared that in so doing there might have been a loss in the length of the ear. Fortunately prolongation is more closely correlated with length of husk than with length of ear. The loss in length of ear has not been material, and the worm-resistant strains have a satisfactory ear length. The average for the different progenies ranges from 15.2 to 26.7 cm. Since little is to be gained by reducing the damage at the expense of the length of ear, it would probably be safer in future work to use length of husks as a basis of selection than to rely on the prolongation.

### HUSK LEAVES

The correlation between damage and husk leaves is 0.31. Since husk leaves afford additional surface on which moths can deposit eggs the larvæ of which may gain access to the ear, a positive correlation would be expected. On the other hand, eggs so deposited are to some extent at the expense of eggs which in the absence of husk leaves would be deposited on the silks. Larvæ hatching on the husk leaves would be somewhat delayed in reaching the ear. These larvæ might be expected to do less damage than those hatching on the silks, and for this reason the damage per larva should be negatively correlated with husk leaves.

That the husk leaves do attract the moths or at least afford a location for the eggs is indicated by the positive correlation of husk leaves with number of larvæ, 0.52. The second assumption of an opposite relation with damage per larva does not appear in the direct correlation, which is also positive though only 0.12. It will be shown, however, that in general as the number of larvæ increase the damage per larva also increases, and the partial correlation of husk leaves with damage per larva for constant number of larvæ is, in fact, negative, −0.32. This makes it appear that there is also support for the view that husk leaves tend on the average to reduce the damage done by each larva.

The final results are therefore in accord with the supposition that the manner in which husk leaves increase the damage is through providing additional opportunities for the moth to deposit eggs near the tip of the ear.

Since the reduction in damage per larva is more than outweighed by the increased number of larvæ introduced into the ear, the practical conclusion is that husk leaves are to be avoided in breeding worm-resistant strains.

The regression of damage on husk leaves is 0.98; that is, an increase of one grade in the husk leaves is attended by an increased damage of nearly one grade or about 10 per cent. This relation is not the result of the slight negative correlations between husk leaves and prolongation or length of husks, since the partial correlation between husk leaves and damage for constant prolongation and length of husks is higher than the direct correlations.

### NUMBER OF LAYERS AND NUMBER OF HUSKS

Number of layers and number of husks are a closely associated pair of characters, the correlation between them being 0.68.

As a protective character number of layers appears to have the advantage. The direct correlations between number of husks and each of the three measurements of damage are negative, but too low to be of significance; and since the correlations of number of layers with the measures of injury are in every case higher, the correlation between number of husks and damage is doubtless largely a secondary relation, owing to the relatively close relation between husks and layers. The partial correlations between number of husks and the measures of injury for constant number of layers are, in fact, all positive instead of negative.

On the other hand, a large number of layers appears to be a protective character second only to prolongation in importance. The direct correlation between number of layers and damage is $-0.52$. Its operation must be largely independent of prolongation, for the partial correlation between layers and damage for constant prolongation is $-0.51 \pm 0.09$. With days to silking constant, the correlation is reduced to $-0.45$ and for both days to silking and prolongation constant the correlation is $-0.40$.

Since the records show that only 4.5 per cent of the larvæ gained access to ears by penetrating the husks, it is difficult to explain the correlation between number of layers and damage as a result of any direct protection. A large number of layers, which, of course, means wide husks, might bring about a closer wrapping of the husks and thus to some extent impede the progress of the larvæ. It seems more probable, however, that the true relation is that suggested as a partial explanation for the relation between prolongation and damage and that number of layers is positively correlated with some protective character not considered in these experiments.

Since the correlation between layers and number of larvæ is closer than that between layers and damage per larva, a large number of layers

would appear to reduce damage more by reducing the number of larvæ than by reducing the damage per larva, and it is difficult to imagine how a number of layers can have any direct effect on the number of larvæ unless the idea is entertained that a large number of closely wrapped layers causes the larvæ to desert the ear.

The relation between layers and number of larvæ is not the result of any relation existing between layers and prolongation, since the partial correlation for constant prolongation is −0.47. The interprogeny regression of number of larvæ on layers is 0.12—that is, the number of larvæ is reduced on the average by 0.12 of a larva with the addition of each layer.

The average intraprogeny correlation for these characters is −0.04, and the regression of larvæ on layers is 0.01.

In Table VIII the inter- and intra-progeny standard deviations, correlations, and regressions of the measures of injury and the more important protective characters are brought together for comparison. The uniformly lower values of the intraprogeny regressions as compared with the interprogeny regressions support the idea that there are other important characters not included among those recorded.

TABLE VIII.—*Inter- and intra-progeny standard deviations, correlations, and regressions of the measures of injury and the more important protective characters of corn*

| Factor. | Standard deviations. | | Correlations. | | | | | | Regressions. | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Prolongation. | | Number of layers. | | Husk leaves. | | Prolongation. | | Number of layers. | | Husk leaves. | |
| | Interprogeny. | Mean intraprogeny. | Interprogeny. | Mean intraprogeny. | Interprogeny. | Mean intraprogeny. | Interprogeny. | Mean intraprogeny. | Interprogeny. | Mean intraprogeny. | Interprogeny. | Mean intraprogeny. | Interprogeny. | Mean intraprogeny. |
| Damage.........per cent.. | 3.74 | 9.77 | −0.71 | −0.26 | −0.52 | −0.10 | 0.31 | 0.01 | −1.02 | −0.72 | −1.72 | −0.51 | 0.97 | 0.05 |
| Number of larvæ.......... | .23 | .58 | −.60 | −.13 | −.51 | −.04 | .52 | .03 | −.54 | −.02 | −.12 | −.01 | .10 | .01 |
| Prolongation.........cm.. | 2.58 | 3.48 | ...... | ...... | ...... | ...... | .... | .... | ...... | ...... | ...... | ...... | .... | .... |
| Number of layers......... | 1.13 | 1.90 | ...... | ...... | ...... | ...... | .... | .... | ...... | ...... | ...... | ...... | .... | .... |
| Husk leaves......grades.. | 1.20 | 2.01 | ...... | ...... | ...... | ...... | .... | .... | ...... | ...... | ...... | ...... | .... | .... |

## MATURITY

A character often ascribed to sweet varieties is that they remain in an edible condition for a longer time than do field varieties. Comparatively little damage is done after the ears have passed the edible stage, and, if the hardening of the grains was hastened, it seems not unreasonable that the injury should be diminished, and this might be a partial explanation of comparative immunity of field varieties. In the 1916 experiments the majority of the ears were harvested between 16 and

18 days from silking. Correlations involving days to harvest and maturity therefore have relatively little significance. The data are sufficient, however, to prove that differences in the rapidity of maturing could not have been an important factor in causing the differences in damage. In no instance was there a significant interprogeny difference in the average maturity at 16, 17, or 18 days from silking. Neither did the two Hopi hybrids, the table variety of soft corn, and the commercial variety of sweet corn, differ significantly in this respect from the worm-proof progenies. The interprogeny regression of the degree of maturity on days from silking to harvest, of 0.72, indicates that for each additional day that elapses the maturity advances on the average 0.7 of a grade. Since it is almost certain that the regression of maturity on days is not linear, the average difference in maturity between the ears harvested at 16 and at 17 days from silking is perhaps a better criterion of the regressions than that calculated from the correlation coefficients. This difference is 1.3 grades of maturity.

It might have been expected that the progenies requiring the longer season to reach the silking stage would also have required a longer time after silking before reaching the edible condition. This proved not to be the case. The correlation between the degree of maturity and days to silking was positive and close, 0.924. This was to a slight extent due to the fact that silking to harvest averaged slightly longer in the late season progenies, but with silking to harvest constant the partial correlation of maturity and days to silking was 0.88. As a further check on this determination the ratio of "maturity" to "silking to harvest" was correlated with days to silking and found to be 0.73.

Two possible explanations are suggested for this unexpected relation:

(1) The field varieties used as parents in the crosses were longer season than the sweet varieties, and field varieties are supposed to mature the seed more rapidly after fertilization. If there was coherence between these two characteristics, the later maturing parents should mature their seeds more rapidly. It should be recalled, however, that with the same number of days from silking to harvest the writers failed to detect significant difference in the degree of maturity among the different progenies or the nonsweet varieties included in the experiments.

(2) The climatic conditions following the flowering of the later progenies may have been more conducive to rapid maturing of the seeds than earlier in the season. It is difficult to find support for this view in the meteorological conditions of the latter part of the season when the days are shorter and the temperatures no higher. It has often been observed, however, that varieties planted late in the season mature with greater rapidity than the meteorological conditions seem to warrant.

## INSTINCTS OF THE MOTHS

That the number of larvæ found in the ears of the different progenies shows significant differences suggests that the moths exercise a choice in depositing their eggs. It is possible to go a step farther and by examining the average amount of damage inflicted by each earworm to determine whether some progenies form a more suitable medium for the larva than others. It would seem that some allowance might have to be made for the crowding of the larvæ and their cannibalistic tendencies, both of which would tend to reduce the damage per larva in ears with a large number of larvæ. It is found, however, that in spite of these factors the correlation between number of larvæ and damage per larva is positive instead of negative—that is, on the average the more larvæ there are in an ear the greater is the damage done by the individual larva. In the light of our present knowledge this would seem to indicate that the instincts of the moth are in accord with the requirements of the larva. In other words, the moth deposits more eggs on the plants most acceptable to the larvæ. The only alternative explanation that suggests itself is that the larvæ desert ears that are distasteful to them.

A further indication that the moths exercise choice in attacking plants is the closeness of the correlation between the extent of damage on first and second ears of the same rows. Since this interprogeny correlation is closer than that between damage and prolongation, the most effective protective character measured, it follows that the close correlation between the damage of first and second ears does not result merely from the fact that both have a similar prolongation.

It might be urged that, since the two ears on a plant frequently come into silk simultaneously, there would be a tendency toward similar infestation. To test this point, the interprogeny correlation between the number of days that elapsed between the silking of first and second ears, and the difference in the number of larvæ found in first and second ears was calculated. The correlation was $0.24 + 0.10$. This correlation, while in the right direction, is too low to explain the similarity of infestation of first and second ears, and may be the result of chance.

If it is correct to assume that a great part of the immunity that has been secured has come about through a correlation between husk characters and some protective character or characters not recorded, it would not be surprising if there were similar correlations between long husks and characters of field varieties that are undesirable in a table corn.

The progenies differed widely in depth of grain and tenderness, but those selected for propagation seem to compare favorably in palatability with their sweet ancestors. Sweet varieties have a larger percentage of sugar than field varieties and the transformation of sugar to starch is

delayed in sweet varieties. It is possible that in these particulars the immune strains might tend to resemble the field parent. So far as has been observed, this has not been the case. Both the percentage of sugar and the retardation of transformation are very difficult to measure accurately, for, in addition to the labor of chemical analysis, the problems are seriously complicated by variations due to the time when the analysis is made and by individual variation. It would seem that, to compare two strains with respect to these characters, it would be necessary to analyze a sufficient number of samples of each variety to secure a reliable average and to repeat this entire process at short intervals, beginning soon after fertilization and continuing until the sugar content was practically constant.

The only evidence obtained on these points is that when gathered at the proper time the immune strains were pronounced by a number of different observers to be fully as sweet as the parent sweet varieties, and that in the regression of maturity on days silking to harvest no consistent differences were found between the immune strains and commercial sweet varieties. That sweet segregates from a cross between sweet and field varieties are not deficient in sugar is shown by the work of Pearl and Bartlett,[1] who found the percentage of sugar in the $F_2$ segregates of a sweet with dent cross to be higher than in the sweet parent.

## CONCLUSIONS

In the southern part of the United States and throughout the Tropics very little sweet corn is grown. The chief reason for this is believed to be the ravages of corn earworm (*Chloridea obsoleta* Fab.).

Attempts to grow sweet varieties in the South usually result in an almost complete destruction of the crop by corn earworms. The native field varieties, on the other hand, escape with relatively slight injury, and are largely used as a substitute for sweet corn.

The most obvious difference between sweet and field varieties that might be expected to affect the activities of the corn earworm is the extent to which the ears are protected by husks. Sweet varieties generally have the husks poorly developed. A possible reason for this may lie in the fact that in the northern part of the Corn Belt one of the most desired characteristics in sweet corn is an early season. Generally speaking, early varieties produce few leaves and few leaves are associated with few husks. There is, therefore, a simple explanation of why commercial varieties of sweet corn have poorly protected ears and the poorly protected ears of sweet varieties afford at least a theory as to why they are especially susceptible to the ravages of the corn earworm.

With these facts in mind the problem was to combine the well-protected character of the ears of southern varieties of field corn with

[1] PEARL, Raymond, and BARTLETT, J. M. MENDELIAN INHERITANCE OF CERTAIN CHEMICAL CHARACTERS IN MAIZE. *In* Ztschr. Indukt. Abstam. u. Vererbungslehre, Bd. 6, Heft 1, 2, p. 1–28, 1 fig. 1911.

the table qualities of sweet varieties in the hope that a sweet variety with some degree of immunity would thus be secured.

Crosses were made between commercial varieties of sweet corn and southern varieties of field corn. Sweet seeds were selected from the first-generation ears, and in the second generation plants with well-covered ears were chosen and propagated. The descendants of these plants have been found to be much less subject to injury from the corn earworm than commercial sweet varieties.

The earworm resistance was tested in 1915 near San Diego, Cal., and in 1916 near Washington, D. C. In both seasons the series of hybrids as a whole was found to be less damaged by the corn earworm than commercial sweet varieties. There were also pronounced differences in the immunity of the progenies derived from the different $F_2$ generation ears. The close agreement between the extent of damage of first and second ears of the different progenies is taken to indicate that the constitution of the plant is an important factor in the immunity. An effort was made to determine the plant characters which give rise to this comparative immunity.

That the factors concerned in immunity are inherited, and are, thus, capable of improvement is indicated by the correlation between the extent of damage in related progenies. The correlation between the average damage of parent and offspring was $0.66 \pm 0.09$.

Low damage was found to be significantly correlated with a number of morphological characters. For the most part these morphological characters were also correlated with one another. Of the characters measured, prolongation, or the extent to which the husks exceed the ear, was found to be the most closely correlated with low damage. The interprogeny correlation between prolongation and damage was $-0.71$, with a regression of 1.02 per cent in damage for each centimeter of prolongation. Within the progenies the average correlation was $-0.26$ and the regression 0.72. This difference between the inter- and intraprogeny regression is believed to indicate that the protection is in part due to other characters correlated with prolongation and not included in those measured.

The thickness of the covering provided the ear by the husks was also found to be associated with low damage, but since only 5 per cent of the larvæ that reach the ear do so by penetrating the husks here again the relation can hardly be a direct one of cause and effect. From the standpoint of worm resistance husk leaves are also shown to be an undesirable character.

By recording the number of larvæ in each ear it is possible to resolve the total damage into (1) number of larvæ and (2) the average amount of injury done by each larva.

It was found that in the more immune progenies both the number of larvæ and the damage per larva were low. Since the number of larvæ must be determined largely by the choice exercised by the moth in depositing eggs, it follows that the plants avoided by the moths are also the plants which the larvæ find most distasteful. This agreement between the instincts of the adult insect and those of the larva is difficult to explain as the result of morphological characters of the plant and would argue that at least a part of the immunity is the result of chemical differences, perhaps the presence of some volatile substance distasteful alike to the moth and the larva. Both in California and Maryland during the period of the experiments the injury from corn earworms was found to decrease slightly as the season advanced.

From the experiments here reported it appears that by increasing the length and thickness of the husk covering and reducing the husk leaves varieties of sweet corn can be produced in which damage from the corn earworm is materially lessened. No difficulty was experienced in securing by hybridization and selection the desired plant characters in combination with the seed characters of sweet corn.